the discocellular veinlet. The Eupterotidæ moreover can at once be distinguished from the Lasiocampidæ by the important character of their well-developed frenulum, this being entirely absent in the Lasiocampidæ. The larvæ of the Lasiocampidæ are densely hairy, often with long thick tufts directed forwards on either side of the head, or backwards from the anal segment, as in the Liparidæ (to which Mr. Hampson considers them allied); whereas the larvæ of the Eupterotidæ are more Arctiid in character, such hairs as there are, whether few or many, being chiefly emitted in tufts from wart-like excrescences.

There can be no doubt whatever, from the entire structure of the moths and the character of their larvæ, that *Anaphe* and *Hypsoides* must be placed in the family Eupterotidæ of Hampson.

XLV.—*The Interpretation of the Sponge Organism, and some Recent Works on Sponges.* By Dr. Otto Maas *.

Since the investigations of F. E. Schulze on the structure and development of sponges paved the way, probably all zoologists have looked upon these animals as *three-layered*, consisting of an outer and an inner layer of epithelium, and enclosed by these a connective-tissue mass with cells and deposits of various kinds. This method of interpretation does not take into consideration the question whether the three layers correspond to the layers which arise from ectoderm, endoderm, and mesoderm in higher animals, and also does not necessitate our holding any particular view regarding the systematic position of sponges. As a matter of fact the adherents of the most divergent theories on this point—both those who derive sponges from a special class of Protozoa separated from other Metazoa, and those who consider them as true Metazoa, but as a special phylum, as well as, finally, those by whom sponges are regarded only as a degenerate branch of the Cœlenterate stem—have all recognized the three-layered structure of sponges in their speculations.

Another question specially referring to the group of sponges would be whether the three layers of the *adult* arise in the development of the individual sponge from three separate

* Translated from a separate impression, communicated by the Author, from the 'Biologisches Centralblatt,' Bd. xii. nos. 18–19, pp. 566–572 (Oct. 1892).

germinal layers or from two only. F. E. Schulze has frequently given prominence to this distinction between the layers of the adult and of the embryo, and has said that sponges can only be regarded as triploblastic animals if, in the undifferentiated embryo and before histological separation, three cell-layers, distinct from one another but undifferentiated in themselves, could be distinguished—a state of things which, to my knowledge, has not yet been demonstrated with certainty in any sponge. However that may be, in the *adult* sponge at all events, since the lead given by Schulze, the covering layers of epithelium have to be sharply distinguished from the third layer, the enclosed connective-tissue substance with its various contained elements.

In this triple division, which is founded on the relative position of the layers and is supported by histological discoveries, a correction has recently been made by Topsent *, which at first sight appears not unimportant, but which, it seems to me, makes little fundamental alteration. This author distinguishes, to begin by summarizing his chief results in this respect, four kinds of cells—referring first to the boring sponges and then to the Halichondriæ—namely (1) cellules contractiles, (2) vibratiles, (3) conjonctives, and (4) digestives pigmentées. The first and second constitute, according to him, the ectoderm and endoderm, the others the mesoderm. By contractile cells he understands those which, as he points out, from their position and appearance have hitherto been regarded as ectoderm and endoderm or as "fibres," the contractile fibre-cells of the mesoderm. When he further says that the latter are the only elements which have been made answerable for the contractility, he does not at the same time take into consideration the fact that contractility and mutability of form have also been usually accorded to the epithelial ectoderm cells. For how can authors otherwise have formed a conception of the opening and closing of pores? Moreover there is to be found in the literature a whole series of special examples, in which reference is made to alterations in the form of the ectoderm cells—by Lieberkühn in *Spongilla*, by F. E. Schulze in *Sycandra*, by myself in the young and by Weltner in the adult *Spongilla*, by Vosmaer in *Myxilla*, and so on. Further, it is not justifiable to comprise offhand in one group the cells of the external skin and the contractile elements in the interior, however similar the two kinds of cells may appear

* Topsent, E., "Contribution à l'Étude des Clionides," Arch. Zool. expér. v. *bis* Suppl.

histologically. The former constitute the covering in the region where the body of the sponge is bathed by the water, but the latter lie *inside* a connective tissue, and hence cannot be termed ectoderm, so far as regards the adult differentiated sponge.

It is somewhat different if we extend our investigation and raise the question whether in the course of the phyletic development of sponges the covering epithelium cells and the contractile elements were not one and the same, and whether we do not find even now a similar relation in primitive sponges, as E. A. Minchin has done *. He has described in the oscula of a calcareous sponge generally held to be of primitive and simple structure a sphincter which contracts these openings so readily that they have hitherto not been seen. This sphincter consists of two epithelial layers of flat, spindle-shaped, ectoderm cells; of mesodermal elements there are only wandering cells to be observed here and there; hence Minchin concludes with reason that here the very energetic contraction is only brought about by the ectoderm. Minchin yields indeed too much to Topsent when he subsequently expresses the opinion that all authors have called the muscle mesodermal; but he applies Topsent's and his own results in a more correct manner when he says "that in a highly specialized sponge muscular cells which originally formed a part of an epithelium became more specialized and sank into the mesoderm."

I find the most developed condition in this respect in the horny sponges, according to F. E. Schulze's well-known description. There "contractile fibre-cells," easily recognizable by their structure, lie in great quantities in the mesoderm, *i. e.* in the connective-tissue mass, often arranged in strands and sometimes forming complete concentric layers round the canals; on the other hand, the covering layer also has become further differentiated, the cells of the epidermis have secreted a fine cuticle, and as far as this extends their power of contraction must be at an end. Thus we have here the division of labour carried to its fullest extent.

On the contrary, we have before us, not only in the sphincter but in the whole structure of *Leucosolenia clathrus*, a more primitive condition, as Minchin's histological discoveries show †. The sponge itself has great power of contraction, and the different forms that have thus arisen were earlier regarded as varieties and then as stages of development. In

* E. A. Minchin, "Oscula and Anatomy of *Leucosolenia clathrus*," Quart. Journ. Micr. Sci. xxxiii. p. 4 (June 1892).

† E. A. Minchin, "Some Points in the Histology of *Leucosolenia clathrus*," Zool. Anzeiger, 1892, no. 391.

reality they are only phases of contraction, which pass somewhat quickly into one another; and if the ectoderm be investigated in different stages of contraction all gradations are found, from an ordinary flat cell (where the sponge is expanded) to completely mushroom-shaped cells, which show the chief mass of the cell-body displaced deeply inwards (where the contraction is very strong). The connective-tissue substance contains no elements for contraction; the wandering cells occurring in it are easily distinguished by their nucleus with nucleolus and their dissimilar contents from the contractile cells with uniformly granulated protoplasm and nucleus with a network. Since besides these there are only spicules with their cells and sexual products to be found in the middle intermediate cell-mass, and as, further, the above-mentioned ectoderm cells appear regularly in a form corresponding to the contraction for the time being, it may be rightly concluded that the seat of contractility in this simply built sponge is still specially in the outer epithelial layer. The simplicity of *Leucosolenia clathrus* is of course shown also in the fact that it does not yet possess any separate flagellated chambers, but that the whole internal cavity is evenly clothed with collar-cells. The latter necessarily take a passive share in the contraction, and then become compressed in transverse diameter, corresponding to the direction of contraction, and hence longer.

Through the discoveries of Minchin as well as of Topsent our attention is again drawn to the question referred to above, raised by F. E. Schulze, as to whether sponges which show three layers in the adult condition are not nevertheless merely diploblastic animals ("Metamorphose von *Sycandra raphanus*," Zeitschr. f. wiss. Zool. Band xxxi., 1878). The two recent authors seek to arrive at a conception of the intermediate layer by the histological method, since they look upon its elements as not equivalent in themselves, but as standing in closer or more distant relation to the primary layers. Topsent's merit appears to me to consist in that he recognizes the contractile cells of the intermediate mass as being much more similar to the covering-cells than are the cells of the intermediate mass among themselves; of the latter there still remain to him as specially mesodermal the *cellules conjonctives* (in which the skeletogenous cells must also be included) and the *digestives pigmentées*. Minchin also has attempted a similar solution of the intermediate layer into its heterogeneous

elements, and after separating out the contractile cells as of epithelial origin, he regards as "mesodermal organs" proper only the skeleton and the genital products. "Cellules digestives pigmentées" he does not mention among them; but these from their function—according to the one author they take up food-stuffs, according to the other they only transport them further from the digesting flagellated cells—must stand in closer relation to the covering of the surface and of the interior, or, rather, become set free directly from it.

However justifiable it may be to apply the histology, especially of a primitive sponge, to the interpretation of the middle layer, nevertheless we may expect still better explanation from the *developmental history*. In the development of *Sycandra* F. E. Schulze has incidentally shown that in this sponge there are present at first in any case only *two* germinal layers, which afterwards form the three layers of the adult, inasmuch as from the flagellated cells of the larva arises only the endodermal system, and all remaining elements spring from the larger non-flagellated cells of the embryo. With regard to this it may be pointed out that he (at that time surely not without intention) enumerates the differentiations of this layer in the same serial order in which, as it now appears, they were laid down both in the ontogeny and phylogeny. He says, for example, "Shall now this layer of tissue thus constituted, in which the skeletal parts arise, the genital cells are formed, and in places even contractile fibre-cells occur, be termed mesoderm, and its outer flat epithelial covering ectoderm, or not?" He arrives at a negative conclusion, because all these elements are differentiated out of *one* embryonic cell-layer. How this indubitable process is carried out in detail has still, as is well known, to be investigated.

In a larva, the structure and metamorphosis of which appear to permit a comparison with *Sycandra*, it was my good fortune to be able to follow * this differentiation somewhat more closely, and particularly to determine how the various elements of the middle layer become separate at different periods of the ontogeny. The larva of *Esperia* (as also a series of other Desmacidonidæ-larvæ investigated by me) consists, apart from complications of detail, in the main of *two* different layers—first of a layer of small and very slender flagellated cells, with minute nuclei, which lie more anteriorly and make up the greater part of the surface of the larva; and secondly of a much more bulky layer of much

* O. Maas, "Die Metamorphose von *Esperia Lorenzi*, nebst Beobachtungen an anderen Schwammlarven," Mitt. d. Zool. Station zu Neapel, x. Bd., 3 (1892).

larger cells, together with spicules, which forms the surface only at the hinder pole, and in addition makes up the interior of the larva. In fixation, which takes place with the anterior pole, the small flagellated cells come to lie in a reversed position in the interior, and the whole remaining mass grows round them. From the former arise the flagellated chambers and the efferent canals in part, while from the cells of the latter are formed all the remaining constituent parts of the sponge.

The separation of *some* of the elements has already been completed in the larva, so that two kinds of cells can be recognized in it and spicules are formed in quantities; but *other* elements first become differentiated after the metamorphosis. The two kinds of cells in the large-celled mass are, first, such cells as are provided with a nucleus and nucleolus and contain deposits of unequal size, and, secondly, cells the nucleus of which shows a network and which contain a uniform protoplasm. From the former arise the amœboid wandering cells, which, as is known, give rise to the genital products; while the latter, with uniform protoplasm, have various destinations. After metamorphosis they for the first time separate into the cells of the outer covering and into the contractile elements, which come to lie in the parenchyma of the intermediate mass; they are thus identical with the "ectoderm," the "cellules contractiles" of Topsent. The separation takes place relatively late; even during the metamorphosis the "mesodermal" muscle-cells and the "ectodermal" covering-cells cannot be distinguished from one another, especially at the marginal parts; their separation first becomes distinct with the formation of the canal-system. In these siliceous sponges also the contractile elements often form whole tracts; the differentiation, however, never goes so far as in the horny sponges; the "ectoderm," *i. e.* covering-cells, never lose their contractility, and throughout life look histologically very similar to the corresponding elements in the intermediate mass.

On this account there is no ground for designating this covering and the contractile elements as ectoderm simply, as Topsent has done, even after I have shown their common derivation. The spicule-forming cells and the amœboid wandering cells might just as well be termed ectoderm. It is true that they are separated in the embryos much earlier than the muscular elements, but this is a difference of degree and not of kind.

On the whole the circumstances are instructive under

which the various tissue-elements are gradually differentiated from the principal mass of the larva which remains after deducting the collar-cells. *First are separated the supporting skeletal substance and the cell material from which the genital products arise. At a later period the epithelial covering-layer and the contractile elements first become separated. Much later still the cells appear differentiated which glue the spicules together into bundles by secretion of spongin.* The ontogeny of *Esperia* furnishes a good indication as to how these must have developed in the course of ontogeny. Naturally displacements and abbreviations in point of time must not be left out of consideration; thus, for example, in the phylogenetic history of sponges the formation of spicules and fixation have universally and with reason been brought into connexion with one another; but a whole series of free-swimming sponge-larvæ show spicules already present. On the whole, however, the sequence of events among themselves and the nature and manner of differentiation may be taken as good guides to conclusions.

The development of *Esperia*, and indeed of *Sycandra* also, has a parallel in the phylogenetic stage represented by *Ascetta clathrus* in the sponge series. In this simple sponge we have, according to Minchin, little more than skeleton and genital products in the intermediate tissue; the seat of contractility lies still especially in the epithelial covering, just as must have been the case, according to the development of *Esperia* and *Sycandra*, in phylogeny, and in very primitive forms must still be.

From a series of cases in which the development of spongin is more accurately known to us we are well justified in speaking of a diploblastic embryo. We could distinguish in it, according to the cases before us, an ectomesoderm and an endoderm; but these names at once entail a comparison with the germinal layers of higher animals, and the preceding discoveries were intended to be kept within the limits of the group of sponges.

Berlin,
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